Adaptive strategies of primates in relation to leaf eating

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Introduction

The most specialized of the primates are the folivores. Among the living prosimians—Platyrrhine and Catarrhine monkeys—two major types of gut specialization for processing leaves have evolved as follows:

(*1*) Large cecum or wide colon in *Lepilemur, Pro-*

pithecus, Avahi, Indri, some Platyrrhine monkeys like *Alouatta* and, to a lesser extent, for Catarrhines like *Gorilla, Symphalangus,* and some Cercopithecidae. In this type of gut, bacterial fermentation provides at least a partial hydrolysis of cellulose and hemicelluloses occurring after the absorption of the largest part of the soluble sugars, fats, and amino acids.

(2) Sacculated stomach in *Presbytis, Colobus,* and *Nasalis,* where the bacteria and flagellae affect the food at an early stage of digestion. This is followed by selective absorption as the digesta move down the gut.

Not only gut morphology, but different strategies of adaptation to the environment which involve behavior and sociology are also important characteristics of leaf-eaters. These feeding strategies related to folivory affect many primate species—in addition to those whose staple food is leaves—because in natural conditions, leaves are the main source of protein for most of the large frugivorous primates.

Several examples are presented below, with a comparison of the ecological niches of these leaf-eating primates in different natural systems.

Prosimians as Folivores

A specialized prosimian folivore.

The sportive lemur, *Lepilemur leucopus,* which lives in the south of Madagascar, provides a rare example of a specialist for leaf-eating among the primates (Figure 1). This nocturnal species, which feeds mostly on crassulescent leaves, reingests a part of its fecal material, just like the rabbit which practices "caecotrophy" (Taylor, 1940). Such a peculiar behavior is unique among the primates (Charles-Dominique and Hladik, 1971), but the other features related to the folivory of the sportive lemur are typical of the other folivorous primates.

The mechanism of digestion of the leaves has been investigated (Hladik et al., 1971). Table 1 shows the progress in concentration and deconcentration of the main components of the leaves during the twofold cycle of ingestion and reingestion by a sportive lemur. The food ingested in natural conditions was a mixture of leaves and flowers of two species of Didiereaceae, no other leaves being available during the dry season. This food was fairly rich in protein (15.1 percent), but poor in lipids (2.7 percent) and reducing sugars. The ratios of hemicelluloses to lignocellulose indicates that very few hemicelluloses are hydrolyzed after the animal begins feeding at night. There is an increase of this ratio in the cecum, showing that a part of the cellulose is rapidly hydrolyzed.

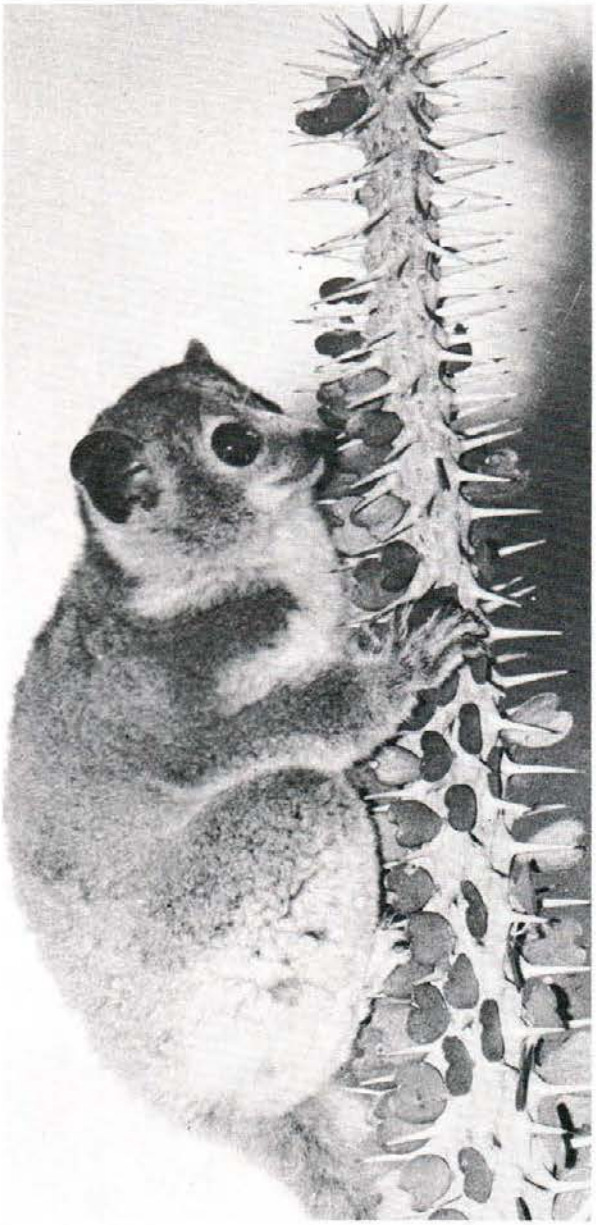

Figure 1. *Lepilemur leucopus* on a Didiereaceae (*Alluaudia ascendens*) from which the leaves can be used as a staple food.

The hemicelluloses are slowly hydrolyzed afterwards and absorbed in the colon where the ratio of hemicelluloses to lignocellulose is progressively reduced.

A large part of the food decomposed in the cecum passes quickly and forms "feces" that could be compared to the "caecotrophes" of the rabbit, containing a high proportion of protein. These particular feces are eaten and pass a second time through the small gut, where absorption of the soluble components resulting from bacterial fermentation occurs. The feces reingested by the sportive lemur have no special shape characteristics, as in the case of the

Table 1. Composition of food and ingesta in the digestive tract of *Lepilemur leucopus*. (From Hladik, *et al.*, 1971.)

	Composition (percent of dry weight)			
	Protein	*Lignocellulose*	*Hemicelluloses*	*Ratio of Hemicelluloses to Lignocellulose*
Natural food ingested (mixture of leaves and flowers of *Alluaudia ascendens* and *A. procera.*)	15.1	24.1	13.6	0.56
Stomach content (at night)	10.3	43.0	23.1	0.54
Caecum content (at night)	45.8	17.5	49.3	2.8
Beginning of the colon (at night)	35.4	29.0	34.5	1.2
Beginning of the colon (afternoon)	36.0	39.9	21.6	0.54
End of the colon (afternoon)	26.9	45.6	20.6	0.45

rabbit, and they are difficult to identify in the stomach content; but the ramified short-chain fatty acids with uneven numbers of carbon atoms that we found in the stomach content can be used as a tracer to demonstrate the reingestion since they are typical of bacterial action and are formed in large quantities in the cecum.

In *Lepilemur*, the adaptation for folivory includes not only morphological and physiological features, but also the very peculiar behavior for a primate, *caecotrophy*. This strategy allows a more complete absorption, in the small gut, of all the soluble substances resulting from bacterial fermentation. Thus, an animal of 600 g of body weight survives on the poorest diet observed among primates. In terms of the calories available in the raw foodstuff before the effects of bacterial fermentation are considered, there is an intake of only 13.5 Kcal per day (Charles-Dominique and Hladik, 1971).

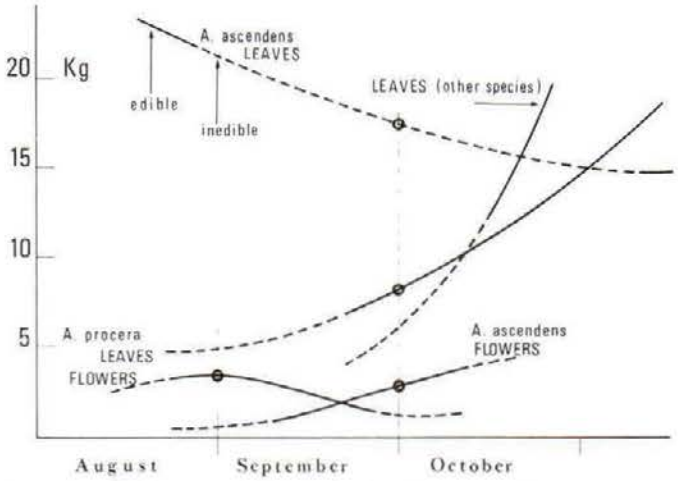

Figure 2. Variations in the food available in the supplying area of one *Lepilemur* during the period of maximal drought.

Socioecology and diet of lepilemur

The utilization of leaves as a staple food involves a social strategy of habitat utilization which is a common characteristic of most of the leaf-eating primates (Hladik, 1975). These convergent socio-ecological patterns are shared by the primate species of different taxonomic groups in which the social organization itself might be more or less complex according to the level of evolution.

Lepilemur has one of the most primitive types of social organization (Charles-Dominique and Hladik, 1971; Hladik and Charles-Dominique, 1971, 1974). The adult males occupy exclusive territories with respect to each other, but the territories of one or more adult females are included in each male's territory. The social groups are thus very small and simple, consisting of 1 adult female with 1 or 2 offspring maintaining periodical contact with 1 male.

Territories of *Lepilemur* generally cover less than 0.2 hectare, which allows very high population densities. We recorded 350 *Lepilemur* per km² in the Didiereacae bush habitat, and 810 per km² in a gallery forest (biomasses of 2.1 kg/hectare and 4.9 kg/hectare respectively).

In the bush habitat, we surveyed the trees along a transect and calculated the average quantity of food available for one *Lepilemur*, during the period of maximal drought (Figure 2). Two species of Didiereacae—which look like big cacti—*Alluaudia procera* and *A. ascendens* form the main part of this bush and produced at this time most of the food available. In these particular conditions, a calculation with good accuracy was fairly simple to perform. We found

an average for each animal of 1.6 times the minimum food necessary for survival (Charles-Dominique and Hladik, 1971). Even among nonfolivores (cf. Smith, 1968), a mammal cannot stay in an area where very little food above the minimum requirement is available.

The above calculation applies only to a period of about 2 months during which a minimum of food is available for *Lepilemur*. Just after that period (Figure 2), new leaves start growing and the stock of potential food is thus rapidly increased. One can suspect, nevertheless, that the size of the territory of *Lepilemur* was selected in relation to the food available during the worst drought periods. This is an inclusive strategy for the species, allowing the maximal efficiency of land use (maximum biomass) without any loss of population during the periodic seasons of minimum food production.

The territorial behavior of *Lepilemur* maintains the population density at an optimum level. The territories are stable, with precise boundaries defended by the owner, who utters loud calls and makes other displays, but rarely directly fights against intruders. With nightfall, the sportive lemurs leave their "nests" located in hollow trunks or in the thickest parts of the bush, and start calling in duets: 2 animals, one on each side of a territorial boundary, together give a series of short, successive calls (Charles-Dominique and Hladik, 1971). The necessity of using sounds for marking boundaries might appear obvious for a nocturnal species, if we suppose that they cannot see the intruders clearly; but it has been demonstrated by Pariente (1974) that *Lepilemur* can see accurately in the light levels of his nocturnal environment. The loud calls for territorial marking may be correlated with the fact that a leaf-eater does not have to move very much to find his food, and thus has only a few occasions for visual displays along territorial boundaries. The sounds are more efficient, especially in small territories. This might explain why vocal display has been selected for in many other leaf-eating primates and why they have many convergent traits.

Other folivorous prosimians

There are several types of dietary specializations among the different prosimian species. The lemurs evolved from a primitive type whose diet included at least a large part of insects and some fruits (Charles-Dominique and Martin, 1970). This primitive animal was probably small and resembled either *Galago demidovii* (weighing 60 g and now living in the evergreen forest of continental Africa), or *Microcebus murinus* (also weighing about 60 g and adapted to different biotopes in Madagascar).

Although fruits are the main food resource for most of the prosimians, leaves are utilized by many species even if they are less specialized than *Lepilemur* or have evolved divergently. Ingesting leaves, at least in small quantities, might be a primitive trait of prosimian feeding behavior since *Microcebus murinus* was observed in natural condition feeding on *Uapaca* leaves (Martin, 1972). Only the large lemur species, nevertheless, utilize leaves in large quantities. This follows the general principles of energetics (McNab, 1978; Parra, 1978) and allometry in body proportions (Grand, 1978). Leaves must be retained in large quantity and for a long time to allow the processes of fermentation. The largest forms are generally the more folivorous, as shown by some examples recently studied in the field.

In places where they lived in sympatry (southwest forests for Madagascar), *Lemur fulvus* and *Lemur catta* feed partly on the leaves of different plant species. Considering the records of individual activity (which are not exactly the true proportions of foodstuffs in the diets), Sussman (1972, 1974) found 89 percent of leaf-feeding by *L. fulvus* and 44 percent by *L. catta*. Body weight for both species is around 2.5 kg. For both species, the food choices may vary according to the vegetation available in different biotopes—*L. catta* diet is described by Jolly (1966) in the gallery forest of the south of Madagascar—but it always includes a fraction of leaves.

Propithecus verreauxi, living in different types of vegetation, has been observed by Richard (1973, 1978). According to the place and the season, this indriid of about 3 kg body weight may feed on large amounts of leaves. Some larger species of *Propithecus*, living in the rain forest of Madagascar and weighing up to 6 kg, also use large amounts of leaves in their diet (Petter, personal communication), but no precise data are available to compare these larger species with the smaller *P. verreauxi*.

The largest of the living lemurs, *Indri indri* (Figure 3), weighs about 9 kg, and inhabits the rain forest of the eastern coast of Madagascar. It feeds mainly on leaf material (Pollock, 1975). From 40 to 70 percent of the feeding observations involve young leaves and buds. Fruits comprise 25 percent of the feeding observations while seeds comprise about 10 percent. Pollock observed the *Indri* occasionally coming to the ground to ingest pieces of dead wood and earth. This phenomenon of geophagy is a common trait of many species of primates which use leaves as staple food (Ripley, 1970; Hladik and Hladik, 1972; Hladik, 1973; Oates, 1974). Geophagy is not related to the mineral composition of the diet but probably its physical structure (Hladik and Gueguen, 1974).

Figure 3. The indri (*Indri, indri*) is the largest of the living lemurs and the most folivorous among them. (Photo by J. J. Petter)

Among the prosimian species, different aspects of gut morphology can be related to leaf-eating. Maximum development of both the cecum and colon is found in the Indriidae (Hladik, 1967), while among Lepilemuridae, only the cecum is expanded.

Body weight and diet in relation to the composition of the natural substances

The adaptations to leaf-eating concerning gut and also tooth morphology (Kay and Hylander, 1978) have to match the environmental conditions. The different foodstuffs available in natural conditions have a range of composition (Table 2) fairly similar in different environments. As a consequence, the range of body size of the prosimians, as well as higher primates, is in relation to the natural diet.

The smallest species have diets yielding the maximum energy, made up of insects and fruits. Whenever several sympatric species of primates include insects in their diet, an individual of any given species foraging in the same area can obtain approximately the same quantity of insects per unit time (Hladik and Hladik, 1969; Charles-Dominique, 1971). Thus the small species (60 to 250 g) like *Galago demidovii, Arctocebus calabarensis, Loris tardigradus,* etc., can fill their stomachs with insects. Larger species cannot obtain enough insects during 1 day (or 1 night) of foraging and they have to fill their stomachs with a complementary type of food, such as fruits, gums, or leaves. For example, *Galago alleni, Perodicticus potto, Nycticebus coucang* (body weight 200 g to 1000 g) or higher primates such as *Saguinus geoffroyi* (500 g) have a diet of insects and fruits. All of the small primates catch as many insects as they can, which makes up 25 percent of the food intake for the small forms but no more than 10 to 20 percent for the larger forms. Leaves can be utilized by a few highly specialized forms of 600 to 1200 g, such as *Lepilemur* and *Hapalemur* (Petter et al., 1977).

The largest species of primates are frugivorous or folivorous. Species weighing up to 2 or 3 kg may use both fruits and insects. For example, *Cebus capucinus* includes 20 percent of insects and other prey in its diet (Hladik and Hladik, 1969). The proportion of insects in the diet of larger primates is generally lower, since the maximum weight of insects collected is limited by their relative abundance. However, the total food intake becomes larger for the larger primate species. Fruits yield an average of only 5 percent protein and the variations between the fruits of different species are small (see Table 2).

The small proportion of insects (5 to 20 percent) included in the frugivorous diet of a large primate is generally not sufficient to increase the protein content above a total of 7.5 to 10 percent of the total dry weight. Such a rate is considered insufficient for a mammal, the minimum for domestic animals being 12 percent protein. Thus, in natural conditions, frugivorous primates around or above 2 kg of body weight are faced with the necessity of finding a complementary protein source. Leaf material is this complementary substance available *ad libitum* in the natural environment. The protein content of mature leaves reaches 10 to 20 percent and the buds and young leaves used by most of the primates contain 25 to 35 percent protein, with the maximum of 55 percent observed in the shoots of a leguminous tree (Hladik et al., 1971; Hladik and Viroben, 1974; Hladik et al., in press; A. Hladik, 1978).

Thus, any large primate species utilizes leaves as the main source of protein because there is no other efficient alternative. If on the one hand *Cebus capucinus* or *Macaca sinica* (3 kg) ingests only 15 percent of green vegetal material (Hladik and Hladik, 1972), then on the other hand, by contrast, larger species like *Ateles geoffroyi* and *Alouatta palliata* (6 and 8 kg) may utilize even more leaves and buds (20 and 40 percent respectively of the total ingested; Hladik and Hladik, 1969). This large proportion of leaves and buds is necessary to compensate for the low amount of protein in a frugivorous diet without any animal food supplement. The diets of *Lemur* and *Propithecus,* described in the previous section,

Table 2.—Some examples of the composition of natural substances eaten by primates in different environments. (After Hladik, *et al.*, 1971, and Hladik unpublished data concerning Sri Lanka [1800 analysis] and Gabon.)

		Percent dry weight		
	LEAVES	*Protein*	*Soluble Glucids*	*Lipids*
GABON	*Baphia leptobotrys*, shoots	55.0	—	—
(rain forest)	young leaves	36.3	20.1	2.2
	mature leaves	26.1	—	1.3
	Ongokea gore	19.3	24.9	1.2
	Gilbertiodendron dewevrei	10.2	13.5	0.7
PANAMA	*Cecropia* sp.	12.5	24.6	2.1
(rain forest)	*Ceiba pentandra*, shoots	25.3	19.5	1.2
SRI LANKA	*Glycosmis pentaphylla*, young leaves	31.5	5.6	3.1
(dry forest)	*Walsura piscidia*, young leaves	19.5	8.3	1.5
	Adina cordifolia, mature leaves	11.8	7.8	7.3
	Alangium salvifolium, shoots	26.2	10.3	2.6
	FRUITS			
GABON	*Nauclea diderrichii*	4.5	47.2	5.3
(rain forest)	*Aframomum giganteum*	8.2	48.8	11.1
	Musanga cecropioides	8.8	31.5	6.3
	Pseudospondias longifolia	7.5	17.4	0.6
PANAMA	*Dipteryx panamensis*	4.4	41.5	1.4
(rain forest)	*Cecropia peltata*	5.0	36.4	2.3
	Ficus insipida	4.5	30.1	3.5
	Spondias mombin	2.8	57.4	0.7
SRI LANKA	*Drypetes sepiaria*	2.8	52.5	7.1
(rain forest)	*Ficus benghalensis*	8.4	6.8	18.1
	Syzygium cumini	6.6	4.1	2.2
	Garcinia spicata	6.2	30.6	20.3
	INSECTS			
GABON	mixed insects from litter	70.2	0.5	3.5
(rain forest)	adult Sphingidae	65.6	1.8	16.3
	Caterpillars (An 15)	62.3	6.4	21.2
	Ants with nest (*Macromiscoides aculeatus*)	29.0	20.0	4.2

consist basically of this same type of fruits and leaf combination.

Foraging for insects may be useless for large primates, since the protein reward would be too small compared to the time and energy required in searching for insects. We do not know exactly why some intermediate-sized diurnal lemurs, such as *L. catta*, have retained the strategy of feeding only on fruits and leaves without utilizing some insects. Could it result from competition with birds? For the largest species of lemuriformes, such as *Indri indri*, the leaf material is the only resource available in large quantity and the fruits and seeds can be considered as a complement for carbohydrates.

This very broad generalization about food composition and primate body weight applies only to the major size categories. Many variations in the diet are related to the combination of more subtle factors like socio-ecology which must be considered in more detail.

Biomass and supplying area

In the different rain forests where data have been fully collected (Leigh and Smythe, 1978; A. Hladik, 1978), leaf production is approximately the same. Other food resources such as buds and young leaves, fruits, etc., are available in smaller quantities, but the order of magnitude is probably similar. In the tropical forests of dry zones, the production is lower than that in the rain forest (approximately half the leaf production; Hladik and Hladik, 1972).

The biomasses of the different primate species are ultimately limited by the food resources. The maximum biomass may be high for a species that feeds on ubiquitous resources like the leaves of the common tree species, or low for a species using scarce resources like leaf flushings and fruits, or even very low for a species that relies on the products of secondary producers, such as insects. Thus, a comparison of the maximum biomasses for a species is a fairly good indicator for the general diets of the different *copus* reaches 5 kg per hectare in the gallery forest of the south of Madagascar, while *Microcebus murinus,* feeding on insects and fruits, accounts only for 0.25 kg per hectare (Charles-Dominique and Hladik, 1971).

To complement this general information, it is necessary to calculate the total food available for 1 individual nocturnal prosimian or for 1 group of diurnal primates and to determine to what extent the local resources are shared by other individual prosimians or by other groups. Generally there are large overlapping parts common to different home ranges (Figure 4). Consider 3 adjacent primate troops, A, B, and C. Let us define 3 classes of habitat utilization: Class 1, 2, and 3. The core area (or territory) will be referred to as Area 1 for groups A, B, and C. In Area 1, each troop has exclusive utilization of all the resources. In the overlapping parts (Area 2), any two groups, such as A and B, share the resources. It has been demonstrated (Hladik and Hladik, 1972) that each group can use an equivalent amount of the food available in a type 2 area. When the ranges of three groups, A, B, and C overlap (defined as a class 3 area), one-third of the resources is available for each group. We define the "supplying area" (*surface moyenne exploitée*) as area 1 + half of area 2 + one-third of area 3 + etc. for a given troop. The larger the home range in relation to "supplying area," the greater the sharing of scattered food resources occurs. This will be shown below by the feeding and social strategies of different prosimian and higher primates.

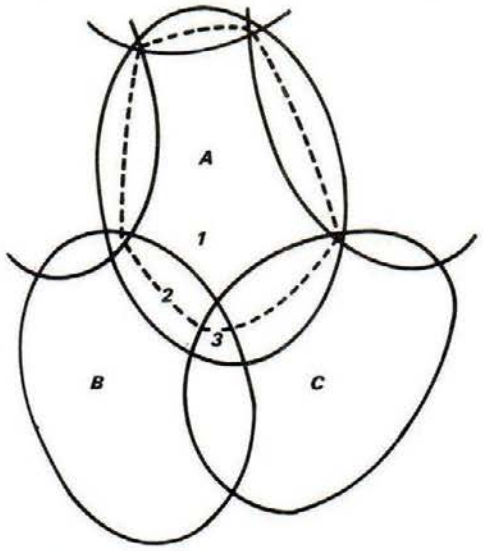

Figure 4. The "supplying area" of group A, as determined by the limits of the home ranges of the other groups (*see text*), is delineated by the broken line.

Socio-ecology and folivorous diet among prosimians

As with morphological structures, the behavioral and social characteristics of the large, diurnal lemuriform species of Madagascar show different trends and many convergences.

The leaf-eaters, *Indri* and *Propithecus*, form the smallest social units that allow a regular distribution of the population in small territories. The *Indri* live in family groups of 3 or 4 (Petter and Peyrieras, 1974; Pollock, 1975), while the *Propithecus* form larger groups of 4 to 6 and show more tolerance among males and among females (Richard, 1974, 1978).

The melodious vocalizations of the *Indri* permit each group to know the location of its neighbors without moving toward the limits of its territory. These calls may act as a repellent between the groups, and thus maintain the territorial boundaries. *Propithecus verreauxi* of different groups may interact visually (Richard, 1978), but they also have a typical territorial call that they utter early in the morning. Many other primates have a territorial call (Gautier, 1975), but the regular use of this loud vocalization by the leaf-eating primates at the beginning of the period of activity is a characteristic of these small, barely mobile groups. As in the case of *Lepilemur,* the vocal display has been selected for use when visual displays have little chance of being efficient.

In the bush of the south of Madagascar, the diurnal folivorous *Propithecus verreauxi* reaches a biomass similar (4 kg per hectare) to that of *Lepilemur leucopus,* which is folivorous and nocturnal (Charles-Dominique and Hladik, 1971). *Propithecus* feeds on a slightly wider variety of plant species on a relatively

larger range (Richard, 1978). The individuals or very small groups of *Lepilemur* utilize the most common plant species, and the relative abundance and regular dispersion of these food resources allow a regular dispersion of *Lepilemur* on small supplying areas.

In the dry forest of the southwest of Madagascar, Sussman (1972, 1974) found a similar clear-cut relation between the ecology and the social organization of the 2 sympatric species of *Lemur, L. fulvus* and *L. catta*. The biomass of *L. fulvus* may be greater than 10 kg per hectare in correlation with a diet including a very high proportion of leaves. This species lives in small groups of from 5 to 10 animals, on a small range (0.75 hectare), and utilizes a small number of common trees (3 species yielded 80 percent of the food). In contrast, *L. catta* lives in larger groups of about 20 animals on a larger range (8.8 hectares), and has a smaller biomass (6 kg per hectare). This correlates with a partly folivorous diet including more fruits. The larger size of the supplying area of this last species is not correlated with the biomass (smaller than that of the previous species), but certainly is correlated with the uneven dispersion of the plant species utilized as food. In fact, Sussman showed that *L. catta* utilizes about twice as many food plants as *L. fulvus*. The very high biomasses that we can deduce from Sussman's observations may reflect the maximum possible utilization of the habitat by the folivorous lemurs, as is the case for the folivorous langurs in a dry forest of Sri Lanka (Hladik, 1977).

Compared to these figures, the biomass of the *Indri* seems very small (around 1 kg per hectare) in the rain forest of the east coast of Madagascar (Petter and Peyrieras, 1974; Pollock, 1975). This must be related to the feeding habits of the *Indri* which eats almost exclusively the young leaves which have attained only about a tenth the weight of their full-grown counterparts (A. Hladik, 1978). Furthermore, young leaf production is not evenly distributed in time. On the other hand, *Indri* feeds on a small number of tree species (82.6 percent of Pollock's feeding records concern 12 species among the 20 common ones out of a set of many hundreds of rain forest tree species).

Platyrrhine Monkeys as Folivores

In Central and South America, the only truly folivorous mammal studied is the three-toed sloth, *Bradypus* (Montgomery and Sunquist, 1975, 1978). Nevertheless, leaves play an important part in the diet of several species of primates.

Howler monkeys

The howler monkey, *Alouatta palliata,* has been described as a folivorous primate in the early literature, owing to superficial observations, but large quantities of fruits are eaten and the leaves can be considered as a complementary part of the diet. We followed a group of howlers during 15 months on Barro Colorado Island, Panama, to make quantitative estimates of the food intake, and obtained a diet including 60 percent fruit and flowers and only 40 percent leaves (Hladik and Hladik, 1969). These round numbers are related to the wet weight and can be considered as low accuracy data (± 5 percent). These data are the only criteria for interspecific comparisons. Even though the feeding times that can be accurately measured are generally not closely related to the food intake by volume (Hladik, 1977), we will compare our data with studies employing time measures. The more recent study of *A. palliata* by Milton (1978) demonstrated the intraspecific variations of the diet of the howler monkey in relation to the local variations of the environment. Her data on feeding (46 percent on fruit and 44 percent on leaves) came from the same group of howlers that we previously observed, and show that the main characteristics of the feeding behavior have been maintained. A small number of food species are selected to form the staple food of that group. *Ficus* is still the main fruit component of the diet.

We discovered that these different *Ficus* species have different amino acid contents in the protein fraction of their fruits and leaves (Hladik, et al., 1971). The mixture of *Ficus* fruits and leaves in the diet of the howler monkey is complemented with many other food species (all of which are not analyzed in such detail), and the data suggest the maintenance of a favorable balance of essential amino acids.

Like any large species of frugivorous primates, the howler monkey (7 to 8 kg) needs the leaf material to maintain a normal level of protein intake and does not intentionally eat any insect or other invertebrate prey. Nevertheless, in the sample that we utilized to calculate the average protein content in the annual diet, we found only 9.6 percent protein.

The variations in the diet of the howler monkey are certainly related to the protein and soluble sugars available in the different food species. Milton (1978) reports that the groups spent 39 percent of time feeding on fairly new leaves and only 5 percent on mature leaves. Glander (1975, 1978) recorded howler monkeys in a relict riverine forest eating new leaves 44.2 percent of the time and mature leaves

19.4 percent. All these records of time feeding are the most accurate data available, but they cannot be compared since they refer to different environments and different samples on which the feeding intake is not predictable. Schlichte (1978) observed the howler monkeys in Tikal, Guatemala, and reported over an interval of 3 months probably the most extreme condition in which they can survive. During his study, the howlers spent 70 percent of their time feeding on fruits of just one species of tree. In this species-poor forest, the animals used only 7 of the 36 species as food sources.

In the rain forest, the feeding strategy of the howler monkey, which is adapted to the fruits and leaves of about a dozen of the common tree species, does not vary to a great extent. Klein and Klein (1975) gave a description of the feeding strategy of *Alouatta seniculus* (in Colombia) which is very similar to that of the howler of Barro Colorado, including the utilization of the immature fruits and leaves of different *Ficus* species.

The maximum biomass of the howler monkey on Barro Colorado Island is about 4 kg per hectare (Hladik and Hladik, 1969). One group of 10 howlers used a supplying area of 15 to 20 hectares. There is a fairly rapid shift in the home ranges of different groups (Chivers, 1969) and, over the long term, one can consider that a very important overlap between the supplying areas of different groups gives access to an important number of scattered tree species for each of the small groups.

The group is of medium size (up to 15 or 20) with little evidence of dominance hierarchy among males. Eisenberg et al. (1972), characterized this intermediate type of social organization as "age-graded male troop," differing little from the smaller "one-male groups" formed by the true folivorous primates. Among the frugivorous-folivorous large lemurs of Madagascar, we also found this type of medium-sized group, except that among lemurs the females were generally less tolerant and the system was closer to a matriarchy.

The loud calls uttered by the howlers, especially at dawn, have an important function in the maintenance of the territory (Carpenter, 1934; Chivers, 1969). When utilizing leaves and very common fruits, like those of *Ficus,* the howler monkeys do not have to travel long distances to feed. Consequently, the loud calls may be the most efficient signaling method they can use.

The choice of a limited number of common food species for complementary nutrients allows the relatively small groups of howler monkeys to share a non-homogenous environment divided into small home ranges, slightly increased by the overlaps. This feeding strategy of a fruit-and-leaf-eater could not be applied to a primate species using more scattered resources without facing the risk of unequal division of the food resources among the groups.

Spider monkeys

The red spider monkey, *Ateles geoffroyi,* is a typical frugivorous primate, weighing 5 to 6 kg, for whom the leaves (especially the young leaves and buds) are a necessary complement of the diet. In the forest of Barro Colorado, the leaves account for 20 percent, (fresh weight) of the annual food intake of the spider monkey (Hladik and Hladik, 1969).

Ateles geoffroyi utilizes a wider variety of food species than *Alouatta palliata* on Barro Colorado Island, where 80 percent of the total food ingested by *Alouatta* is made up of 14 tree species, while about 25 tree species account for the same proportion of the food of *Ateles.* The supplying area of a group of *Ateles* is also wider (40 hectares; Hladik and Hladik, 1969) and the biomass rarely exceeds 1 kg per hectare. Very similar differences were observed by Klein and Klein (1975) between *Alouatta seniculus* and *Ateles belzebuth* in the rain forest of Colombia.

Red spider monkeys obtain most of their protein from leaves. They choose the young leaves and shoots with high protein content—for example, *Poulsenia armata* or *Ceiba pentandra* shoots containing 25.3 percent protein (dry weight). They eat some mature leaves and petioles of *Cecropia,* which contains only 12.5 percent protein, but the leaf petioles are generally selected for their high mineral content (Hladik and Gueguen, 1974). The fruits selected by *Ateles* are richer in soluble glucids than the few species utilized by *Alouatta* (Hladik, et al., 1971). The utilization of food sources that yield more nutrients but are not so common as those resources used by *Alouatta* correlates with the smaller biomass of *Ateles* and its larger home range.

There is a considerable interindividual tolerance and a splitting of *Ateles* populations into subgroups (Klein and Klein, 1975). This behavior trait correlates with the use of scattered food sources.

Capuchin monkeys

The white-throated capuchin, *Cebus capucinus,* is sympatric with the 2 former species on Barro Colorado Island, and is a smaller cebid weighing about 3 kg. It obtains a large part of its dietary protein from insects and small invertebrate prey for which it forages. Nevertheless, 15 percent (wet weight) of its diet

consists of leaves, shoots, and other green vegetal material. This intake is completed by 65 percent fruit and 20 percent invertebrate and vertebrate prey (Hladik and Hladik, 1969). The average composition of the annual food intake includes, by dry weight, 8.8 percent animal protein and 5.6 percent vegetable protein (Hladik, et al., 1971).

This primate species selects the richest parts of a set of food plants that includes more than 40 tree species. The capuchins form large groups with a more obvious social hierarchy than in the above New World species (Oppenheimer, 1968), and their biomass in the rain forest of Barro Colorado reaches only 0.5 kg per hectare. To gather their food, concentrated in small areas over a very wide range of 90 hectares, the capuchins have to travel long distances every day. They have frequent contacts with the neighboring groups; these contacts involve aggressive displays, but no use of loud territorial calls.

Rufus-naped tamarin

The rufus-naped tamarin, *Saguinus geoffroyi*, is a small callitrichid weighing only 0.5 kg. It feeds on fruits and insects, with animal prey accounting for 30 percent (fresh weight) of its diet. Nevertheless, about 10 percent of its diet includes leaves and green plant material. The protein intake of the tamarin includes 16 percent animal protein and 4.6 percent plant protein (dry weight). Obviously, leaves are not very important as a nutrient, but the fact that the tamarins belong to an early diverging group of New World primates and do eat some leaves may suggest that the adaptation to a diet complemented by leaves is a primitive trend which has been amplified in the different primate radiations.

Cercopithecids Tending to Folivory

Near Makokou, Gabon, at the field station of the C.N.R.S., 17 species of primates live in sympatry. Among them are different examples of leaf-eaters, but the only true folivorous mammals of the Gabonese rain forest are the flying squirrels (3 species of *Anomalurus*, 1 of *Idiurus*, and 1 of *Zenkerella*), and the tree hyrax, *Dendrohyrax dorsalis*. This last species, subjected to a short field study (Richard, 1964), showed the relative stability of small individual territories and the use of loud calls probably as a spacing behavior. *Dendrohyrax* was observed in a pen defecating always at the same place.

The small nocturnal prosimians of the Makokou forest include 5 species which have been studied during 7 years by Charles-Dominique (1971, 1975). Their diets include none or very few leaves. A very small proportion of leaves is utilized by *Galago demidovii*, one of the less specialized forms. Two other prosimian species feed on the gums of trees and lianas. For *Euoticus elegantulus*, gums account for 75 percent of the food intake (Charles-Dominique, 1977). These gums are compounds of pentoses and are highly polymerized. They yield roughly the same nutrients as fruits, but necessitate bacterial fermentation, as for digestion of leaves. In this respect, the wide cecum of *Euoticus* has a converging shape and may be compared to the cecum of *Lepilemur* (Charles-Dominique and Hladik, 1971).

Cercopithecinae of Gabon

Among the 8 species of frugivorous Cercopithecidae living in the rain forest near Makokou, the smallest one, *Miopithecus talapoin* (1 to 2 Kg) eats the largest proportion of insects. According to Gautier-Hion (1971), only 8 percent of leafy material was found in the stomach contents. A large band of 115 talapoins lives on 140 hectares with a biomass of around 1 kg per hectare.

Different species of *Cercopithecus* (*C. pogonias, C. cephus*, and *C. nictitans*) can be classified in a range of body weights from 2 to 7 kg. All of them eat fruit complemented by leaves and insects in different proportions. These monkeys may form polyspecific groups sometimes joined by the talapoins (Gautier and Gautier, 1969) and use a large supplying area. There are slight but clear-cut differences in the diets of these three species of *Cercopithecus*. *C. pogonias* includes with fruits an average of 14 percent insects and 2 percent leaves; *C. cephus* utilizes 10 percent insects and 8 percent leaves; *C. nictitans*, the largest species, is also more folivorous, with 8 percent insects and 28 percent leaves (all results from dry weight of stomach contents from Gautier and Gautier, 1975). The total biomass of the polyspecific association described by the Gautiers reaches about 2 kg per hectare, which proves the equal efficiency of this system of fruit-and-leaf-eaters, compared with the systems in other types of environments where the food resources are not so scattered.

The DeBrazza monkey, *Cercopithecus neglectus*, inhabits the river banks of the Makokou forest and forms small groups of about 4 individuals (Gautier, personal communication). Its diet includes some leaves, fruit, and seeds, and is still subject to analysis. It might be similar to that of the black colobus, *Colobus satanas*, living in the coastal forest of Cameroon (McKey, 1978). The population density of *Cercopithecus neglectus* is very high, and the biomass

may reach 4 kg per hectare (after Gautier and Gautier, personal communication). The small groups are barely mobile and are in a small territory. A loud vocalization (a kind of booming typical of other *Cercopithecus* species but more developed in *C. neglectus*) is used at regular intervals. These characteristics of the social structure might be only a convergence toward the social forms shown by leaf-eating primates. The convergence is also evident in a comparison of the digestive system (Hladik and Chivers, unpublished data), and in the fact that they feed on certain types of food with a high fiber content, such as *Gilbertiodendron dewevrei* leaves, which contain only 10.2 percent protein and 13.5 percent sugars (Table 2) and are not eaten by the other primate species.

Two *Cercocebus* species, *C. albigena* and *C. galeritus,* inhabit the Makokou area. In fact they occur in sympatry, but the geographic area of 1 species extends toward the east and west, while the other (*C. galeritus*) extends only towards the east. *C. galeritus* was the subject of a detailed field study (Quris, 1975), showing that its habitat is almost exclusively limited to the fringe of forest along the rivers. A group of 10 to 15 has a home range of about 200 hectares extended in a long strip of 4 to 8 km along a river. There are important overlaps in the ranges of 2 groups and the supplying area is about 100 hectares. The diet of *C. galeritus* is made up of fruits complemented by 13.9 percent leaves and 2.8 percent insects (dry weight of stomach contents, after Quris, 1975). The feeding strategy is similar to that of the larger species of *Cercopithecus,* since the leaves serve as the main protein complement in an environment where the food sources might be equally scattered. The body weight of *Cercocebus* is about 10 kg and the biomass 1.5 kg per hectare (these figures are maximum biomasses in the areas effectively utilized by the primates, not in the whole rain forest including different types of environments).

The mandrill, *Papio sphinx,* is the largest of the Cercopithecidae living in Gabon. Its diet includes fruits, seeds, insects, and a certain quantity of leaves. Large groups of mandrills utilize a very large supplying area (Jouventin, 1975). The field conditions did not permit a detailed study of the feeding strategy, but one can expect that the leaves play an important part in the amino-acid balance, as shown below for the chimpanzee.

Two species of the Colobinae, the black and white and the black *Colobus,* also occur in the forest of Gabon. These folivorous monkeys have been hunted for years; they are still scarce and we do not have good data concerning their ecology. Examples of the ecology of the Colobinae are presented in subsequent sections.

Comparative data from East Africa

A comparison can be established between the primate ecology in the rain forest of Makokou (typical of West Africa) and in the Kibale forest (as an example of East Africa) where detailed field studies have been carried on by T. T. Struhsaker and coworkers (Struhsaker, 1975, 1978; Rudran, 1978; Waser and Floody, 1974; Oates, 1974). The Kibale forest is higher in elevation (1450 m) than the Makokou forest (500 m) and its ecosystem as determined by the number of all species is slightly less complex.

The folivorous monkeys account for the largest part of the biomass of the Kibale forest: *Colobus badius* (17.6 kg per hectare) and *Colobus guereza* (0.6 kg per hectare; figures after Struhsaker, 1975). The red colobus, *C. badius,* eats a small amount of fruit (4.8 percent of the feeding observations), which may represent a larger fraction of the actual food intake by weight. *C. badius* utilizes the young leaves of a limited number of tree species (10 species account for 75.4 percent of feeding observations; Struhsaker, 1978). Groups of 50, which include several males, range over 15 to 20 hectares. Conversely, the black and white colobus, *C. guereza,* forms groups of about 10 concentrated in small areas (2.75 hectares) where they feed almost exclusively on 3 food plants (69 percent of the feeding observations), among which 1 species, *Celtis durandii,* accounts for 48.5 percent (Oates, 1974). Shoots and young leaves account for 58 percent of intake. This less mobile species uses a booming roar which may serve to space the groups (Clutton-Brock, 1975). The difference in the biomass data of Struhsaker between the 2 *Colobus* species is due to the unequal distribution of *C. guereza,* which is located in drier places than the *C. badius* in this nonhomogenous environment. The maximum biomasses of *C. guereza* found in dry areas may be equal or higher (18 kg per hectare; Oates, 1974) than that of *C. badius.* As shown previously, the higher the maximum biomass (considered in an homogenous environment), the higher the proportion of ubiquitous food resource in the diet, since leaves are more abundant than fruits and mature leaves are more abundant than shoots and young leaves.

The 3 *Cercopithecus* species of the Kibale forest, *C. ascanius, C. mitis,* and *C. lhoesti* (1.6, 1.3, and 0.1 kg per hectare respectively), can be compared to the species of the Makokou forest in terms of feeding strategy and resulting biomasses (Struhsaker, 1975; Rudran, 1978). All of these species are frugivorous

and use a large amount of leaves.

Cercocebus albigena forms groups of 15 ranging on 34 hectares (Waser and Floody, 1974) in the Kibale forest. The species biomass for the whole area is 0.6 kg per hectare (Struhsaker, 1975), but the maximum biomass is quite similar to that of *C. galeritus* in the Makokou forest.

The chimpanzee, *Pan troglodytes sweinfurthii,* is sympatric with all the previous species in Kibale, with a biomass of 0.3 kg per hectare.

Anthropoids as Folivores

Chimpanzees and gorillas are still abundant in the rain forest of the Makokou area, but the study of the wild populations of these anthropoids is not yet possible and very few direct observations have been published. These protected animals are extremely shy owing to the recent and continuing hunting pressures. In the field station of Makokou, we worked on anthropoids reintroduced into their natural environment on different islands along the Ivindo River. The ecological studies of semitame animals allowed a very detailed inventory of the diet of the chimpanzee, *Pan troglodytes troglodytes* (Hladik, 1973).

Chimpanzees

The average annual diet of the chimpanzee contains (in fresh weight) 28 percent leaves, shoots, and stems; 68 percent fruits and a few seeds; and 4 percent insects or small prey. When we investigated the composition of these foodstuffs, it was clear that the importance of leaves and shoots was balancing the amount of proteins in the diet (Hladik and Viroben, 1974). In the regular daily intake, leaf proteins are combined with some insect protein. Among the chief plant species eaten throughout the year, the amino acids are partly complementary; for instance, the leaves of *Baphia leptobotrys* contain very small amounts of leucine and threonine, while the shoots and stems of *Hypselodelphis violacea* have larger proportions of these amino acids in their protein. The relative proportion of histidine, leucine, lysine, and threonine is, nevertheless, too low in the protein of the whole plant fraction owing to an excess of valine (Table 3). The small amount of animal protein, from ants of different species, seems to just compensate this lack, but the diet would have a lack of cystine if the insects were not mixed with the plant protein.

Even in populations of chimpanzees which hunt for small-sized game (Teleki, 1973), leaf-eating is compulsory. This is necessary because the protein intake over a year from game is very low and prey is often not available to subadults (Wrangham, personal communication). This explains why the chimpanzees can afford to work for hours to gather the tiny leaf buds of *Baphia leptobotrys* (Figure 5) which weigh 0.05 g but contain 55 percent protein (dry weight).

Table 3.—Comparison of the relative proportions of the essential amino-acids in the vegetal and animal food samples accounting for most of the dietary protein ingested by the chimpanzee, *Pan troglodytes troglodytes*, in the forest of Gabon. The percentages of essential amino-acids are related to their sum. The "total average" is calculated according to the importance of each sample in the diet of the chimpanzee. (From Hladik and Viroben, 1974.)

Amino-acids	*Stems of Hypselodelphis violacea*	*Leaves of Baphia leptobotrys*	*Ants nest of Macromiscoides aculeatus*	*Ants and grubs of Oecophylla longinoda*	*Total average*	*Protein of egg as reference*
Cystine	4.55	7.7	2.7	1.75	5.86	4.8
Histidine	4.75	2.85	9.0	6.55	4.28	4.55
Isoleucine	10.95	11.5	11.3	12.4	11.59	10.4
Leucine	20.25	13.5	19.2	22.1	16.23	16.7
Lysine	10.45	8.65	12.9	15.0	10.36	13.9
Methionine	4.6	2.7	3.4	3.5	3.10	6.1
Phenylalanine	11.45	8.65	8.1	7.6	8.69	11.55
Threonine	11.75	7.9	11.3	10.2	9.01	9.25
Tyrosine	6.05	9.0	8.7	8.4	8.57	9.25
Valine	15.2	27.6	13.4	12.4	22.34	13.5

Figure 5. Chimpanzee, *Pan troglodytes troglodytes*, in the rain forest of Gabon, collecting the tiny shoots of *Baphia leptobotrys* (55 percent of protein content).

Figure 6. Gorillas reintroduced on a small island near Makokou. As leaf-eaters, they need a large amount of bulk and practice coprophagy whenever the leaves and stems are not available in sufficient quantity.

They feed throughout the year on *Baphia* leaves which yield 21.3 to 36.3 percent protein varying with the season. The geophagy which is regularly practiced by the chimpanzee, as well as by many folivorous primates, may facilitate the absorption of the leaf tannins (Hladik and Gueguen, 1974).

The supplying area of the forest-living chimpanzees is very large (Reynolds and Reynolds, 1965) in relation to the distribution of the trees producing large amounts of fruits. Nevertheless, the biomass is about 1.5 kg per hectare, very similar to that of the other primates using leaves as a complement for a frugivorous diet.

Gorillas

An adult gorilla (*Gorilla gorilla*) weighs about 4 times as much as a chimpanzee and can reach 200 kg; it is no longer arboreal at this stage. It feeds mainly on leaves and stems with fruits always being a smaller fraction of the diet. The main field studies concern the mountain gorilla, *G. gorilla beringei* (Schaller, 1963; Casimir, 1975; Fossey and Harcourt, 1977), but little is known about the lowland gorilla, *G. gorilla gorilla*, which may utilize more fruits in addition to the leaves (Sabater Pi, 1966; D'Arcy and Hladik, in preparation). Schaller described more than 100 plant species utilized by the mountain gorilla and watched some regular sequences of geophagy. A limited number of plant species accounts for a large amount of the food intake and, for long periods, bamboo shoots of *Arundinaria alpina* formed 90 percent of the diet of a group (Casimir, 1975). These bamboo shoots, rich in tryptophane, are a good complement for the protein of the leaves and bark of the other food species with which they are mixed in small quantity throughout the rest of the year.

The diet of *Gorilla* involves a large amount of bulk (lignin, cellulose, etc.) and some correlative differentiations of the digestive tract. The wild specimens examined have a relatively larger hindgut than all the species of primates that feed on fruits and leaves (Chivers and Hladik, in preparation). As a consequence of this adaptation, a large volume of fodder is required for a normal behavior. Coprophagy may be practiced under conditions of low food availability. For example, some reintroduced gorillas, living on too small an island near Makokou, destroyed most of the lianas and edible trees. As a result they were not able to find enough leaves to feed on. Every day, they ate their feces which contain much fiber (Figure 6) and perhaps some protein to recycle, as is the case for *Lepilemur*. In Rwanda, *G. g. beringei* also eats its fecal material when bad weather does not allow sufficient foraging time (D'Arcy, personal communication).

According to the field data of Schaller (1963) and those of Fossey and Harcourt (1977), the biomass of the mountain gorilla may vary from less than 1 kg per hectare to 2 kg. This is small when compared to other folivorous primates, but is probably related to the open type of vegetation. We do not have any comparative data for the rain forest of Gabon.

Hylobatidae

The gibbons and siamang have been studied in the rain forest of Malaya by Chivers (1971, 1973). Their comparative socio-ecology parallels the differences and similarities found among other primates feeding on leaves and fruits (Hladik and Chivers, 1974).

The white-handed gibbon *Hylobates lar,* is the smallest species (4 to 7 kg), feeding on fruits 70 percent of its feeding time. A family group of gibbons has a territory of about 50 hectares; thus the biomass is about 0.4 kg per hectare.

The siamang, *Symphalangus syndactylus,* is the largest species (10 kg). It spends 50 percent of its feeding time eating the leaves and shoots of many trees and vines; thus the amount of fruits ingested is smaller than that of the previous species. Among those fruits, the siamang may eat large amounts of immature fruits of different species of *Ficus.* Its feeding strategy resembles the strategy of the howler monkey; this convergence between the 2 species is also apparent in the ranging pattern. A small family group of siamangs is barely mobile in a small territory of 15 to 30 hectares, and the territorial calls, long-carrying in the rain forest, have a spacing function more apparent than those of the other gibbon species. The territories are separated by a buffering zone which lowers the total density of the siamang population. If we consider only what is effectively the supplying area for the groups in a study area, the maximum biomass may reach 8 kg per hectare (Chivers, 1973).

The socio-ecological patterns related to habitat utilization vary with the relative proportion of leaves in the diet. The siamang is more folivorous than the gibbon and forms small, barely mobile groups, and utilizes the most common food sources (Chivers, 1973). In the forest of Malaya, the leaves are used as staple food by the two sympatric species of *Presbytis, P. obscura,* the dusky leaf monkey, and *P. melalophos,* the banded leaf monkey (Curtin and Chivers, 1978).

The Colobinae

With a sacculated stomach and its associated bacterial flora and fauna of flagellates (Kuhn, 1964), the Colobinae show the best adaptation to leaf-eating among primates. The convergence toward the ruminant type of gut was demonstrated by Moir (1967), and the efficiency of such a system allows the utilization of mature coriaceous leaves as staple food. Nevertheless, all the species of Colobinae observed in the field utilize a certain amount of fruits or some seeds.

The ecology of 2 species of *Presbytis, P. senex* and *P. entellus,* have been investigated with respect to the particular use of the chemical environment. These 2 leaf-monkeys live in sympatry with 2 other primate species, *Macaca sinica* and *Loris tardigradus,* in the semideciduous forest of Polonnaruwa, Sri Lanka (Hladik and Hladik, 1972).

The purple-faced langur

Presbytis senex, the purple-faced langur, has been studied at the Polonnaruwa field station by Rudran (1970, 1973). This is a large species (12 kg) socially organized in "one-male groups" of 5 or 6 monkeys. They always stay in the canopy and do not move very much within a small territory of 3 to 4 hectares. The territorial loud calls of *P. senex* are related to intergroup spacing (Figure 7).

Figure 7. A group of *Presbytis senex* in the forest of Polonnaruwa. This group lives in a very small territory (1 hectare) and resources available are the minimum for survival.

The very high biomass of *P. senex* in Polonnaruwa (14.5 kg per hectare) can be related to a highly folivorous diet based on the most common tree species. This diet includes, in fresh weight, 60 percent leaves and shoots, 12 percent flowers and flower buds, and only 28 percent fruits (Hladik and Hladik, 1972).

One individual *P. senex* eats about 400 kg (fresh

Table 4.—Total food in kilograms (fresh weight) available per year for 1 monkey of the different groups of *Presbytis senex* in Polonnaruwa. (After Hladik and Hladik, 1972.)

	Adina cordifolia		*Schleichera oleosa*		*Other trees*
Groups	*Leaves*	*Flowers*	*Shoots*	*Fruits*	*Leaves*
A	1,300	60	240	65	1,100
B	3,500	160	380	105	2,200
C	2,100	100	420	115	2,200
D	4,700	215	350	100	2,000
E	3,500	160	510	160	2,000
F	1,000	50	200	55	2,800
G	6,500	300	300	85	5,800
H	600	30	130	35	1,000

weight) in 1 year. This is approximately one-tenth of what is available, if we consider the supplying area of each group and divide the total food available by the number of individual monkeys within a supplying area (Table 4). The calculation of the production of the different foodstuffs was made on an area of 54.5 hectares by a systematic recording of all the tree canopies and appropriate measures of production (Hladik and Hladik, 1972).

Eating one-tenth of the food production might be the maximum permissible for a folivore that utilizes a fairly large amount of shoots and young leaves (20 percent of the total food intake), without endangering the food plant population. In fact, in the supplying area of group H, which was reduced by the pressure of the dominant neighboring groups, the annual food available per monkey is less than 2000 kg (Table 4) and some trees of this area (*Alangium salvifolium*) were dying because the young leaves were eaten too frequently. Fitzgerald (1978) also found 1 tree species (*Metrosideros robusta*) killed by overbrowsing by the brush-tailed opossum (*Trichosurus*) recently introduced in New Zealand. The ecological adaptation of this opossum cannot be compared with that of the purple-faced langur because the opossums in the whole area feed too actively on 1 preferred tree species. This is a classical danger of introducing new species. One can expect that, in a similar manner in the past, several tree species have been exterminated when new forms of folivores colonized. The situation of *Presbytis senex* in Sri Lanka is the result of a long-term balance between the food species and the folivores. The tree species actually available are not overbrowsed, except by one group—which obviously will disappear. The normal situation of groups A, B, C, etc., is to maintain territories with little overlap (Rudran, 1970), including an average of 10 times or more of the food actually required.

The territorial system of *P. senex* allows a fairly homogenous distribution of the food resources among the different groups (Table 4). If we consider that the most common food resource may be different for different groups, then the small intraspecific variation of the diet may be related to local variations of the food available. This is the case for the howler monkey, *Alouatta* (Milton, 1978). Only a dozen tree species produce 90 percent of the food ingested by *Presbytis senex* and 2 of them, *Adina* and *Schleichera*, account for half of this food. The homogenous distribution of the common food plants allows each group to get its share in a fairly small supplying area (Hladik and Hladik, 1972). The ecology of the black and white colobus in Africa (Oates, 1974; McKey, 1978) is very similar to that of the purple-faced langur.

The gray langur

Presbytis entellus, the gray langur, inhabits the dry forest of Polonnaruwa, in sympatry with *P. senex*. This big colobine of about 15 kg forms large "age-graded male groups" of 20 to 30 individuals living in territories of 10 to 15 hectares (Ripley, 1967, 1970). There are important differences in the ecology of the 2 langur species, one of the most apparent being the reduced arboreality of the gray langur, which spends much time foraging or resting on the ground.

The diet of the gray langur is less folivorous than that of the purple-faced langur, but it includes more shoots and young leaves. The yearly average in fresh weight is 48 percent leaves, 7 percent flowers, and 45

Table 5.—Annual mean production in Kg (fresh weight) available for one individual of the different groups of *Presbytis entellus* for some of the most common food-producing tree species of the Polonnaruwa field station. [The identification as male or female of some *Drypetes* trees was not possible after the period of production; thus some figures are underestimated.]

	Walsura piscidia	*Drypetes sepiaria*		*Ficus spp.*	*Schleichera oleosa*
	shoots	*shoots*	*fruits*	*fruits*	*fruits*
North group	40	180	23.5	62.5	30
Central group	20	135	20	262	115
South group	(few)	>50	>10	197	40

percent fruits. Nevertheless, the maximum biomass of *P. entellus* is quite similar to that of *P. senex*, i.e., about 14 kg per hectare. Both species utilize shoots and young leaves. These are available to be cropped only in limited quantity and may be the limiting factor on langur biomass. Many fruits are utilized by the gray langur, when they are available; since they can be replaced by leaves when not available, however, they are not the core of the diet.

There is more variety in the food choices of *P. entellus* as compared to the monotonous diet of *P. senex*. Ninety percent of the food of *P. entellus* is made up of 25 plant species and 6 of them account for half of the total diet (versus 12 and 2 for *P. senex*). Several plant species are eaten by both langur species, but the proportions differ and there is no competition. For instance, the main food plants of *P. senex, Adina cordifolia* and *Schleichera oleosa,* account only for a small amount (4 and 3 percent) in the diet of *P. entellus* (Hladik and Hladik, 1972).

Some of the plant species eaten by the gray langur are not very common and the territorial system of large groups in fairly large areas is necessary to prevent the unequal distribution of unevenly scattered food sources (Hladik and Hladik, 1972). The differences in the spatial distribution of the main food trees used by the 2 sympatric langur species appears clearly in previously published figures (Hladik and Hladik, 1972).

According to what is eaten by the gray langur, the food available was calculated within the "supplying area" of each of the groups living at the Polonnaruwa field station. These total resources, divided by the number of monkeys in each group, are distributed fairly evenly, when taking into account the slight intraspecific dietary variations (Table 5). A system of small territories would have necessitated more overlaps in troop ranges to allow an equal access to the scattered food resources. On the other hand, the system of large groups with large territories is necessary as an antipredator device, to increase the level of vigilance of partially ground living primates (Crook and Gartlan, 1966). The red colobus is the African ecological equivalent of the gray langur, with only slight differences in the ranging pattern (Struhsaker, 1975, 1978).

Food choices and food composition among langurs

In both langur species, the food choices vary throughout the year, according to the food resources available in the different seasons. These annual variations (Figure 8) have been plotted on a graph according to the total food intake (fresh weight) observed at different seasons for *Presbytis senex* and *P. entellus* (Hladik, 1977). In the total annual food intake, *P. senex* utilizes more mature leaves (about 40 percent) than *P. entellus* (20 percent), which eats a higher proportion of shoots and young leaves. It is remarkable that, at any time of the year, the same type of difference characterizes the diet of each of the langur species. *P. entellus* is more frugivorous and eats more young leaves than mature leaves.

P. entellus which includes more species in its food choices is also more selective, choosing the fruits when they are available and the younger leaves instead of the mature ones. As a result, its diet yields more protein, more lipids, and more soluble glucids. But the seasonal variations have a stronger effect on the diet of *P. entellus* than on that of *P. senex*. The results of the analysis of the different food samples (Hladik, et al., in prep.), show the seasonal content in nutrients presents very little variation for *P. senex* (Figure 9), but large seasonal differences in the dietary pattern of *P. entellus*. In *P. entellus,* the rate of protein intake may be as low as 10 percent (dry weight) of the food intake, reaching 16 percent during the rainy season when the leaf buds and flushing

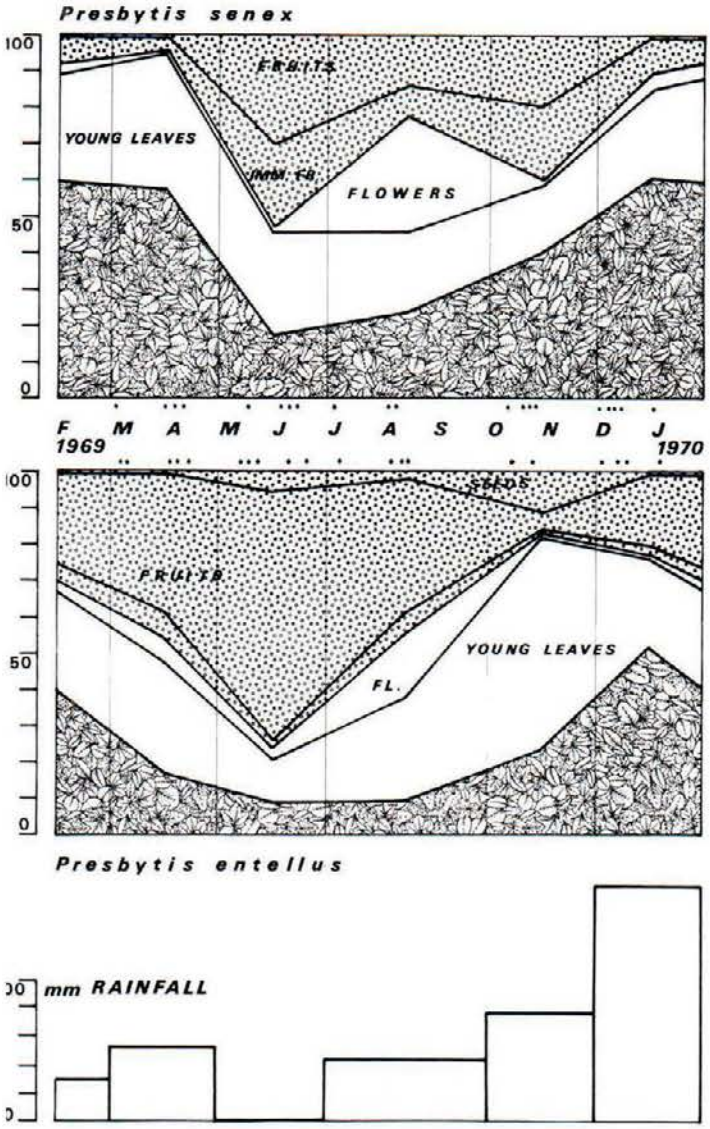

Figure 8. Seasonal variations in the natural diets of *Presbytis entellus* and *P. senex*, in relation to the rainfall which determined food availability during the period of study. Data were collected during continuous daily observations, noted as dots along the time axis. From bottom to top, the food categories are mature leaves; young leaves and shoots; flowers; immature fruits; mature fruits; seeds.

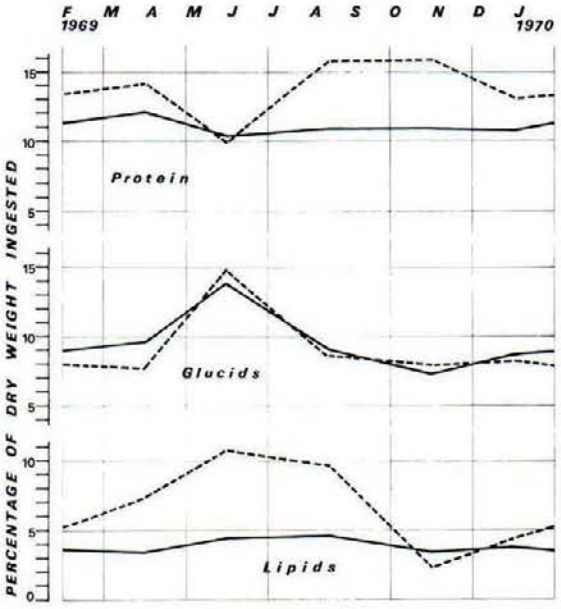

Figure 9. Annual variations in the composition of the diets of *Presbytis senex* (solid line) and *P. entellus* (dashed line).

are very abundant. Conversely, for *P. senex,* the protein content never exceeds 12 percent but is very stable. Similar differences between the langur species appear in the rates of intake of lipids, soluble glucids, and minerals, but the highest average rate is that of *P. entellus.*

As a result, *P. entellus* obtains much more energy from its environment, but it has to spend more energy than *P. senex* to find its more scattered food resources. As is the case for the other leaf-eating primates that feed partly on fruits, the gray langur is more mobile in its ranging and may have more frequent agonistic interactions with the neighboring groups along the territorial boundaries (Ripley, 1967); thus, feeding strategy and social strategy are complementary. The less mobile system of *P. senex* functions with more economy and without any change during the year.

Both langur species eat small amounts of earth. This geophagy which has been observed among most of the primates feeding on large amounts of leaves may have no connection with the mineral nutrition (Hladik and Gueguen, 1974). The mineral content of the earth samples is smaller than the content of the food samples for both sodium and zinc, which are the only elements that might be too low in the total diet.

Conclusions

Primary compounds versus secondary compounds

The selection of the natural food substances by different primate species can be related to their content in primary nutrients (soluble carbohydrates, lipids, and protein). Moreover, many alleochemics (Whittaker and Feeny, 1971; Janzen, 1970, 1978), like tannins, alkaloids, saponins, glycosides, etc., are present in the leaves and in different parts of the plants and some of these chemicals have been selected as repellent or toxic agents against leaf predators. The taste of these chemicals may act directly as a repellent against folivorous mammals. For example, a young gorilla observed in Makokou fed on different liana

leaves on which the screening tests were negative (A. Hladik, 1978). A few other leaves had been chewed and then spat out and, for those leaves, the screening tests were positive, showing the possible presence of alkaloids.

Among many species of rainforest plants, the proportion of species with a high alkaloid content is very low (A. Hladik, 1978). Only 2 to 5 percent of the plant species might have high alkaloid levels possibly resulting from selection due to insect predation and may thus be toxic for mammals. In most of the leaves of the rain forests, the small amounts of alkaloids detected by the screening tests are less toxic than coffee is for man.

Tannins are present in some leaves and Feeny (1969) demonstrated in vitro that the binding of tannins with the protein of the leaves prevents their digestion by trypsin. This would not apply to primates with a microbial gut flora, as for example the Colobidae and *Lepilemur*. For the other species, large quantities of tannins may be a deterrent. We also have suggested (Hladik and Gueguen, 1974) that the soil rich in clay eaten in small quantities by most of the folivorous primates may act as an adsorbent of the tannins. This hypothesis originated with the observation of the utilization of clay with acorns by human populations that would otherwise not be able to eat the tannins of the acorn without this preparation.

The selection of secondary compounds as a plant adaptive strategy resulting from predation by insects is well documented (Janzen, 1978), especially for seeds. It is not obvious for leaves and especially for the leaves of the species of the rain forest, but there is another kind of plant adaptive strategy that can be caused by insect predators. This involves plant parts which are very poor in nutrients. These parts will then be positively selected by insect predators which will neglect them and look for other types of food. Thus, the poorest composition will be selected for in different plant species subject to predation. This strategy is complementary to the retention of toxic allelochemics by the plant parts that have a high nutrient content.

The most specialized folivorous primates can utilize those plant species with a low nutrient content, thanks to a physiological (and sociological) strategy such as the system described for *Presbytis senex*, specialized on *Adina cordifolia* leaves; probably the same situation pertains for *Colobus guereza* feeding on *Celtis durandii* leaves (Oates, 1974). These leaves yield very little nutrient (Table 2). The primates, like other mammals, have a territorial strategy that in most cases prevents overbrowsing. This adaptation is probably very recent, and there is probably very little selection for allelochemics due to the activities of folivorous primates.

The small amounts of nontoxic allelochemics in plants might have an important role in primate feeding behavior. The particular taste, even what humans have found to be very bitter or stringent, is a conditioning stimulus which might complement the long-term reaction of the folivorous primates and improve their efficiency in food-searching.

The role of the primary compounds is obvious when we consider the composition of the natural substances selected by the many frugivorous and partly folivorous primates, since the higher the content in soluble glucids and protein, the more positive the food selection by the primates (Hladik et al., in preparation, and unpublished data from Gabon and Madagascar). The secondary compounds have a secondary role in most of the cases on which we have collected precise data. One case, in our Sri Lanka study (Hladik and Hladik, 1972), concerns the fruits of *Strychnos potatorum* eaten by *Presbytis entellus* and not eaten by *Macaca sinica* which, however, eats the leaf petioles of this *Strychnos*. We found some unidentified alkaloid (not strychnine) in the fruits and nothing in the leaves, but very small amounts of alkaloids have been found in the 76 other leaf samples screened (Hladik et al., in preparation). Thus, the monkeys only need to avoid a few toxic plant species; the rest of their strategy is to balance their diet with different amino acids if they do not have a bacterial flora to synthesize those essential nutrients, or to detoxify the rare harmful allelochemics.

Ecological classification of the leaf-eating primates

The primate species can be distributed into 3 grades divided into finer ecological categories, according to their natural diet (Hladik, 1975), Eisenberg (1978) presents a general classification of the Mammalia in which those categories fit.

The first grade (Figure 10) concerns species utilizing the secondary production as a main source of energy. It includes the typical insectivores and different forms utilizing fruits and insects in different proportion.

The second grade concerns the primate species whose diet combines insects (or other prey) and some green plant parts, such as leaves, and eventually some seeds, as a protein complement for fruits. These species are from genera such as *Cebus, Cercopithecus, Macaca, Papio,* and *Pan*.

The third grade concerns species utilizing the primary production only. It includes the frugivorous and folivorous primate species obtaining their proteins

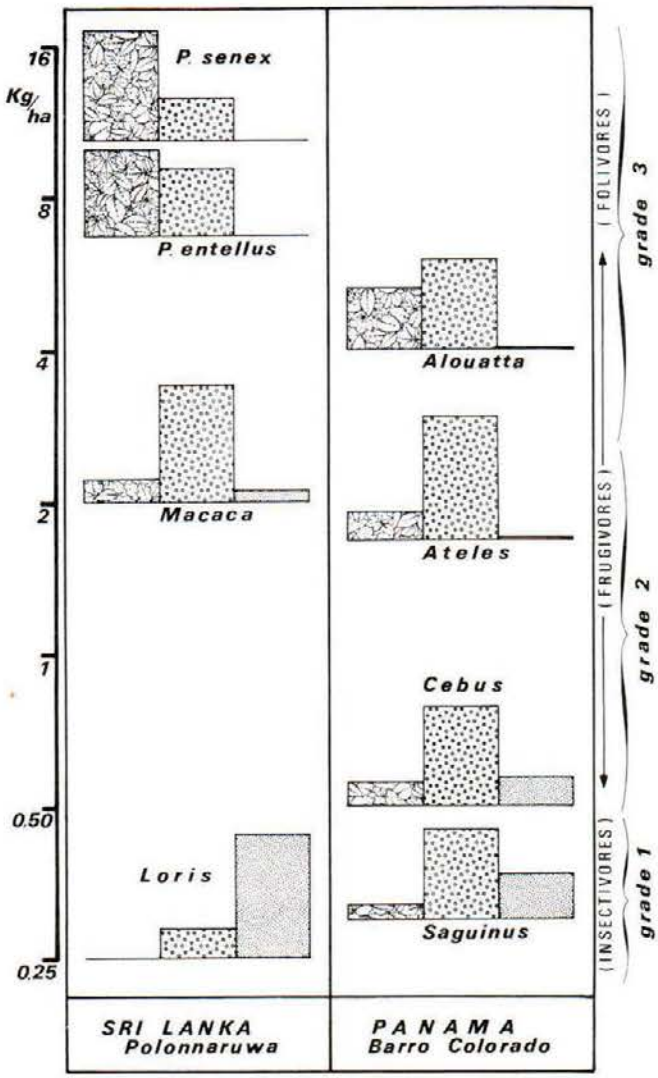

Figure 10. Relationship between the type of diet and the biomasses of primates in two different field stations. The different species are located on a vertical scale, according to the biomass observed in the field. For each species, the diagram represents the proportions of different food categories ingested in one year: leaves (left rectangle); fruits and seeds (central rectangle); insects and other prey (right rectangle). The three grades refer to the ecological classification of the diets presented in the discussion.

essentially from the leaves (*Ateles, Alouatta, Gorilla*). In this category, there is a progressive trend toward forms with either a large cecum and colon (*Lepilemur, Indri*), or a complex stomach (*Presbytis, Colobus*).

The evolution toward a partial or total folivore has occurred in several families of primates and in several parts of the world. In the different radiations, the body weight and the digestive tract have evolved simultaneously. The possibility of utilizing young leaves with a high protein content permitted the emergence of the large primate forms. In the rain forest, the complementarity of leaf phenological patterns of trees and lianas is the main factor on which those primates are dependent (A. Hladik, 1978). The most specialized folivorous primates are adapted to the most ubiquitous resources, that is, the leaves of some common trees that may have escaped insect predation by maintaining a composition with a minimum of nutrients.

There is a limit in the maximum biomass that the folivorous primates can attain. This level is reached when the animals eat about one-tenth of the food available in their supplying area, during a yearly cycle. This condition is the limit for an adequate balance between the food tree species and the monkeys: it has been selected to allow the maximum biomass, as demonstrated for *Lepilemur* and for 2 *Presbytis* species. This level is maintained by the territorial social system. The biomasses of ecologically equivalent species of primates are roughly similar in different forests. This is not surprising when the leaf production is almost the same, as in Gabon (A. Hladik, 1978) and in Panama (Leigh and Smythe, 1978). The folivorous primates crop a very small amount of the total leaf production: about 0.5 percent in the rain forest of Barro Colorado, and 4 percent in the dry forest of Polonnaruwa (Hladik and Hladik, 1972) where the tree species utilized are the most common ones. This low figure for the rain forest is related to the low production of shoots and young leaves and maybe to a selection of a small number of tree species; most of the animal forms are more specialized in the rain forest.

The utilization of common tree species or of the more scattered food sources is another important point correlated with the size of the home range and the extent of the overlaps which allow a homogenous distribution of the food resources in the different supplying areas. Thus, in the different grades (Figure 10) the slight differences in biomasses are related to slight ecological differences, either the proportion of leaves in the diet and/or utilization of common tree species.

It is not possible to say whether the evolution of the social structure resulted from the pressure of the ecological conditions or if the adaptation to the environment followed sociological evolution. It can be said rather that the co-evolution of sociology and ecology was necessary for the emergence of the leaf-eating primates.

Summary

A few specialized forms of primates utilize leaves as a staple food. For many other primate species, includ-

ing apes, the green vegetable fraction of the diet balances in different ways the intake of protein and the possibility for combination with the other available resources.

Among prosimians, *Lepilemur* is presented as an example of extreme specialization for folivory, with a primitive type of social organization and the smallest individual territory. The "supplying area" of the other prosimian genera is correlated with the relative proportion of leaves and fruits in the diet and with the body weight. A general law concerning body weights and diets of prosimians and simian primates is presented and discussed.

The frugivorous-folivorous simian primates show a similar pattern of ecological and sociological adaptations, as exemplified by the genera *Alouatta* and *Ateles* for whom leaves are required to provide adequate levels of dietary protein. A similar feeding strategy is also found in many cercopithecid genera. The "supplying area" and the maximum biomass are thus related to different models of habitat utilization which influence to a large extent the type of social organization.

The feeding behavior of the *Presbytis* and of other folivorous primates depends on primary compounds present in the natural substances. According to the latest data from field and laboratory studies, the secondary compounds play a secondary role in primate ecology.

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